MESOZOIC INSECTS OF QUEENSLAND.

No.4. Hemiptera Heteroptera : The Family *Dunstaniidæ*. With a Note on the Origin of the Heteroptera.

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(Plate lix.; and Text-figures 17-22).

In 1916, I described(3) the beautifully preserved wing of *Dunstania pulchra* Till., from the Upper Trias of Ipswich, Queensland, and placed it as the sole representative of a new family *Dunstaniidæ* within the Order Lepidoptera. This decision had the concurrence of Dr. A. Jefferis Turner, of Brisbane, and was based mainly upon the presence of eight longitudinal veins in the fossil, this being the number found in the hindwings of Frenate Lepidoptera.

While the description of this fossil was going to press, I happened to be on a visit to Brisbane. A day or two before I left, Mr. Dunstan showed me four other specimens bearing the label "*Dunstania*" in pencil; these had just been discovered at Ipswich. Two of them were broad wings resembling the type, and two were much longer and narrower wings. Thinking that these latter must be the forewings of the same insect as that whose hindwing I had assumed the type to be, I added the note on p.32 of the paper quoted above. However, when I received from Mr. Dunstan, later on, the complete collection of Ipswich Insects of which these wings formed a part, and had time to work at them in detail, I soon found that the two narrow wings did not belong to *Dunstania* at all; so that there remained only the two broad wings for study in connection with the original type. Neither of these is in anything like as good a state of preservation as the type is, and one of them is very poorly preserved indeed.

Meanwhile the publication of the original description had created considerable interest amongst entomologists, and discussion soon became rife as to its true affinities. In August, 1916, Mr. E. Meyrick, F.R.S., contributed a paper on the subject*(2), in which he argued strongly against the admission of *Dunstania* to the Order Lepidoptera, and suggested that its affinities might rather be with the Homoptera. He reasoned as follows :—"In order to appreciate the position, I looked up the record of *Palæontina oolitica* Butl., from the Jurassic, hitherto the oldest known Lepidopteron, ... ; I must express my opinion that there is little doubt it belongs to the *Hepialidæ*. . . . . Now it is clearly proved on structural grounds that the *Micropterygina* (the small group to which the *Hepialidæ* belong, otherwise termed Jugatæ) were the primitive form of the Lepidoptera, and the nature of *Palæontina* is in accord with this conclusion and confirmatory of it. Parenthetically, I take occasion to notice that Goss, Tillyard, and others are troubled as to what the early Lepidoptera can have fed upon, when flowering plants were not yet in existence, and honey was not available; it is a problem easy of solution, since the more primitive forms (including the *Hepialidæ*) have in general no proboscis or feeding apparatus, and, therefore, fed on nothing in the perfect state."

"With the evidence recounted above, *Dunstania*, if regarded as Lepidopterous, is violently discordant. As the hindwing possesses neither frenulum nor prominent basal angle of costa, it must be assumed that the forewing was furnished with a jugum; all existing Lepidoptera exhibit one or other of these structures. But all jugate Lepidoptera have the hindwing similar in neuration to the forewing, with at least 11 veins, whereas this wing seems to be of the modern 8-veined type, though conspicuously different from any known form, and in fact quite as highly specialised as any now existing. Finally, there is the apparently corneous margin round the costa and termen, which is altogether abnormal, no other Lepidoptera showing a

* See also "Nature," No. 2488, Vol. 99, Sept. 28th, 1916, p.75, where this paper is reviewed.

trace of it, and in my estimation a far more important systematic character than the two which the author lays stress on."

"It appears to me, then, that this specimen can only be regarded as Lepidopterous on the theory that it is a member of an entirely unknown line of development of that Order, which had attained a high degree of specialisation at a period far anterior to the earliest certainly Lepidopterous insect known, itself a lowly organised form; this cannot be termed impossible, but it involves a very great improbability. The alternative view that the resemblances are accidental and the insect not Lepidopterous seems to me, on the whole, less improbable."

"I cannot venture to express any positive opinion on its possible relation to other Orders, but I suggest that there are some points of resemblance to the Hemiptera-Homoptera, some species of which have a semi-Lepidopterous facies. The corneous margin of the wing, the central cell (usually, it is true, much larger), and approximate number of veins rising from it, and even the curious dark banding of the membrane alongside the veins, can all be paralleled in this group, which, moreover, is already known to have been in existence since the Carboniferous period."*

Mr. Meyrick's criticism led me to study intensely the various types of Lepidopterous wing-venation extant, about which I knew very little at the time that I first described the fossil. I very soon became convinced that *Dunstania* was not a Lepidopteron; but that conviction was not based, for the most part, on the argument set forth by Mr. Meyrick, which I regard as unsound in several important particulars.

Firstly, as regards *Palæontina*. The latest authority on the family to which this fossil belongs is Handlirsch (1), who gives a masterly treatment of this and allied fossils, with photographs and restorations of a number of types, in some of which the hindwing is complete enough to allow of definite proof that the *Palæontinidæ* were most certainly not *Hepialidæ*, as Meyrick avers, nor even Jugatæ of any kind, but definitely Frenatæ allied

* This is surely an error. No true Homoptera were known below the Lias, until I described *Mesojassus* from the Ipswich Trias, and, later on, two new genera from the Permian of Newcastle, N.S.W.

to the *Limacodidæ*. If Mr. Meyrick "turned up the record of *Palæontina oolitica*," how is it that he ignored Handlirsch's epochal work, which does not fit in with his own opinions?

I accept without any doubt whatever Handlirsch's proof that the *Palæontinidæ* were Frenate moths, though I take leave to doubt that they were as closely allied to the *Limacodidæ* as he imagined. The evidence of the hindwings, which are small, with only eight or nine veins, is conclusive on the point. Consequently, there is no absurdity in supposing that Frenate types might have existed also in the Lias, or in the Upper Trias of Australia. That being so, all this part of Mr. Meyrick's argument rests upon an unsound basis.

There is, therefore, no *a priori* reason why a Frenate moth, of a type *far removed* from those we know at the present day, might not also have been in existence in the Upper Trias at Ipswich, though I am quite willing to admit that it might not be a very probable supposition.

Secondly, as regards the "apparently corneous margin" round the costa and termen. In my description, I simply called this "a wide margin without pits," and added that "the external border, or *termen*, shows signs of a delicate transverse ribbing" which "extends also somewhat indistinctly round the apex on to the costa." I purposely refrained from suggesting that it was a corneous margin, as it seemed to me to be equally likely that it had been formed by the crushing down of the deep bases of insertion of a series of stiff and closely packed marginal hairs or bristles, such as one sees in many Diptera, for instance. There was no inherent improbability that such a margin might not be found on a strongly-built and hairy-winged, primitive Lepidopteron.

If, however, the margin be really corneous, then I admit that the character is of great importance, and definitely rules *Dunstania* out of the Lepidoptera. In the actual fossil, the appearance of this margin is certainly not such as to suggest a positive solution to this question, one way or another; but Mr. Meyrick, of course, had only my drawing to go upon.

Thirdly, I should like to reply to Mr. Meyrick's parenthetical

statement that the early ancestors of the Lepidoptera took no food in the imaginal condition. This argument defeats itself. For, if these insects took no food as imagines, then surely their descendants must have even more aborted mouth-parts than their ancestors, and thus they should all be either *Hepialidæ* or *Saturniidæ*! Surely the ancestors of those Lepidoptera that are, to-day, of the haustellate type were originally of the weak mandibulate type still preserved in *Micropteryx* and allies, and were, therefore, pollen-feeders and lappers-up of dew and rain-drops, as the great majority of the Planipennia, Mecoptera, Trichoptera and Diptera are to-day!

To my mind, the great argument against *Dunstania* being a Lepidopteron is simply this, that the venation, quite apart from the mere number of the veins, does not show any of the typical arrangements of that Order, whether Frenatæ or Jugatæ. As soon as I had sufficiently mastered the wing-venation of the Order, I became convinced of this, and definitely rejected my original placing of the fossil. It is part of the object of this paper to relate how the opinions of different entomologists, looking at the problem from different points of view, favoured the claims of various Orders to receive this fossil; but none, including myself, who had the type-specimen itself to study, succeeded in finding the true solution, which was at last given by the study of the new material.

Starting from Mr. Meyrick's suggestion that *Dunstania* might be Homopterous, I find that a number of correspondents entertained this idea, the strength of which lies, of course, in the interpretation of the margin of the wing as corneous. However, Mr. J. Edwards, of Cheltenham, England, an acknowledged expert upon this Order, wrote to Mr. Meyrick, and also to me, strongly opposing the idea, on the ground that he could see nothing in the fossil to indicate such a relationship. As the Homoptera are well represented in the Ipswich Trias by forms differing entirely from *Dunstania*, and as I was unable to establish a single venational character common to the two types, I soon abandoned any idea of relationships in this direction.

In correspondence, other entomologists discussed with me the

probable affinities of *Dunstania*, but their opinions were not published. In particular, I desire to mention Mr. Herbert Campion's share in the clearing up of the mystery. It was through his unfailing courtesy that I was kept in touch with the trend of opinion in England on the fossil, and from him I obtained valuable suggestions as to clues that were worth following out. One of the most interesting of these, originating with Mr. Durrant of the British Museum, and stated in publication by Dr. Bather, F.R.S., in the course of a short review of my paper in "Nature,"* was, that the venation of *Dunstania* might be compared with that of certain groups of Diptera, such as the *Psychodidæ*. At about the same time, Dr. C. J. Gahan, of the British Museum, had before him a small collection of insects from New Zealand, and suggested to Mr. Campion that the fossil should be compared with the Anthomyiid *Exsul singularis* Hutton, which it closely resembles in the shape and general appearance of the wing.

Acting on these suggestions, I put myself into communication with several New Zealand entomologists, in the endeavour to obtain material of *Exsul*. This, however, was not easy to get, as the fly is exceedingly rare, and regarded as a great prize. After a considerable time, I obtained two specimens, one from Mr. David Miller, Government Entomologist of New Zealand, and an expert Dipterologist, and another from Mr. G. V. Hudson, of Wellington. To both of these gentlemen I offer my cordial thanks for their generosity in sending me such valuable material.

While I could not admit any affinity between *Dunstania* and the *Psychodidæ*, I was impelled to study more closely its possible affinity with *Exsul*, in spite of some cardinal differences in the venational scheme, which would be hard to explain on any hypothesis. Believing that I had here, at last, a good solution of the problem, and wishing to give due credit to those to whom the suggestion was originally due, I wrote to "Nature,"† stating my adherence to the probable Dipterous nature of *Dunstania*. However, it was necessary to carry out a very detailed study of

* "Nature," No. 2441, Vol. 97, Aug. 10th, 1916, p.489.

† "Nature," No. 2488, Vol. 99, July 8th, 1917, p.373.

the fossil before anything could be published. Here I was helped and guided by a regular correspondence with Mr. Miller. He, like other entomologists, found in the supposed corneous border of the wing a stumbling-block to the acceptance of any theory of Dipterous affinity for the fossil. He also pointed out the remarkable difference between the structure of the costal vein in *Dunstania* and in *Exsul*, and finally declared his belief in the Homopterous nature of the fossil.

The only other possibility that occurred to me was, that *Dunstania* might be the wing of a large Oligoneurous Mayfly. The shape and venation of the wing made this likely; but I was unable to follow this line of research far, as I soon became convinced that the evident toughness and strength of build of the *Dunstania* wing could not possibly have belonged to the wings of any representative of the Order Plectoptera.

Here, then, after having reviewed possible affinities with four Orders, Lepidoptera, Diptera, Homoptera and Plectoptera, I abandoned the study of this puzzling fossil for a time, in the hope that a respite from the work might rid my mind of any preconceived notions, that were bound by now to be present, after so long a time spent in thinking over the problem, and might allow some new light to come in.

In the meanwhile, I had received from Mr. Dunstan the complete series of fossils found at Ipswich since my first paper had been published, and had been arranging these for study. For some months, I had put the new material of *Dunstania* by, as it was evidently in very poor preservation compared with the type, and I did not expect to get any new evidence from it. It was, however, from this new material that the solution of the problem came; and that solution was of such a nature that it could have scarcely been suggested as a possibility, on the evidence of the type alone.

The number of the type-specimen was 2*a*; the two wings of *Dunstania* received after the type had been described were numbered 107*a* and 147 respectively. In the present paper, I propose to give a complete description of the new material, together with a re-examination of the type in the light of the

new evidence, and an attempt at a complete restoration of the wing.

Specimen No.147 is in a very poor state of preservation, and represents practically the same area of the wing as is found in the type. It clearly belongs to a somewhat larger insect than the type; and, as the venation differs from that of the latter in some important respects, it will form the type of a new genus within the family *Dunstaniidæ*.

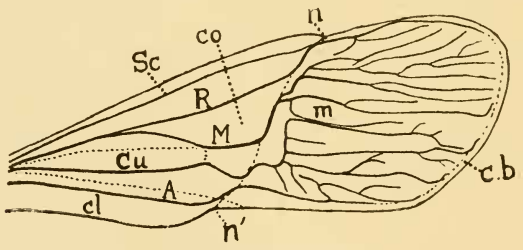
Specimen No.107*a* is in much better preservation than No. 147, but it is not so well preserved as the type. The apical part of the wing is missing, but the whole of what was taken to be the basal part in the type is fairly well preserved. On the other side of this there is preserved a large flattened area, with only traces of disconnected venation. On making a careful drawing of this, and trying to establish its connection with the rest of the wing, on which the venation is well preserved, it became at once apparent that this new fossil represented almost the whole (excluding the base and apex only) of a huge Heteropterous hemelytron, and that the supposed almost complete wings preserved in the type-specimen and in No.147 were, in reality, nothing more than the distal membranous half of the hemelytron, which is separated anteriorly from the basal half, or *corium*, by a strongly developed *node* upon the costa.

With this new and unexpected light upon the problem that had been exercising me for so long, the mystery of the affinities of *Dunstania* became cleared up in a moment. There cannot now be any doubt that these fossils are Heteropterous; the only question that remains for discussion is as to what, if any, recent or fossil families of Heteroptera show any affinity with them.

Before the fossils, including the type, can be correctly described in terms suitable to their new position, it will be necessary to examine them very carefully, with a view to trying to establish the homologies of their unique venation upon the Comstock-Needham system. This is a difficult task. I propose, therefore, to use the new names under which I shall describe the two new fossils at the end of this paper, in order to facilitate the discussion that must take place before those descriptions can be properly given.

Specimen No.107*a* is to be made the type of a new genus and species, *Dunstaniopsis triassica*, n.g. et sp., while specimen No. 147 will also be the type of a new genus and species, *Paradunstania affinis*, n.g. et sp. All these are evidently members of the same family, *Dunstaniidæ*, the venational differences being, at the most, only of generic value.

In discussing the venation of the *Dunstaniidæ*, we shall make use of the most complete specimen, *Dunstaniopsis triassica*, n.g. et sp., supplemented by the type of the family, *Dunstania pulchra* Till. It will be necessary to compare the venation on the corium of the former with the tracheation to be found on the same area of the hemelytra of recent Heteroptera. Unfortunately, few reliable figures of the latter are available. I have selected as the most suitable for our purpose the excellent figure of the tracheation of the nymphal forewing of *Syromastes* (family *Coreidæ*) given by Handlirsch (1, Atlas, Pl. vii., fig.3). It is not necessary to figure the corresponding venation in the imago, as it only differs from that of the nymph in the greater differentiation between corium and membrane, the dividing line becoming a complete whole, and effectually concealing the connections between the veins on the corium and those on the membrane. Consequently, such an archaic type as *Dunstaniopsis* is more closely comparable with the tracheation of the nymphal wing of *Syromastes* than with the venation of the imaginal wing.

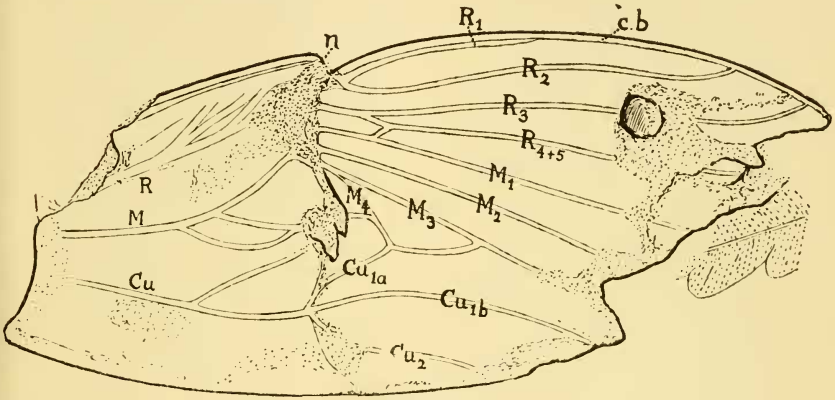


Text-fig.17.

Tracheation of forewing of nymph of *Syromastes* sp.; (×8). After Handlirsch. For lettering, see p.592.

Text-fig.17 shows the tracheation of the nymphal wing in *Syromastes*. The wing consists of a hard coriaceous basal half,

called the *corium* (*co*), and a softer membranous distal half, called the *membrane* (*m*). These are separated by the *dividing line*, running somewhat obliquely across the wing from the *node* (*n*) on the costa to the *antinode* (*n'*) on the dorsum. Posterior to the corium is a narrow projecting anal area, known as the *clavus* (*cl*). Around the membrane is a complete *coriaceous border* (*c.b.*), such as we have already noticed very prominently in the type-specimen of *Dunstania*.



Text-fig. 18.

Hemelytron of *Dunstaniopsis triassica*, n.g. et sp.; (×2·8). Upper Triassic, Ipswich, Q. For lettering, see p.592.

Turning next to *Dunstaniopsis* (Text-fig. 18) we see that the node is more prominent, but that the dividing line is, on the whole, not so clearly marked, and its course is far more irregular. This line also runs more transversely across the wing in *Dunstaniopsis* than in *Syromastes*; but, in many recent Heteroptera, especially in the family *Pentatomidæ*, it takes a similar transverse course, though much straighter than in *Dunstaniopsis*. A further point of difference is that no true claval area can be seen in *Dunstaniopsis*. But, as the extreme base of the wing is not preserved, there may well have been a short clavus present on the lost part.

Turning next to the venation, we notice that, in *Syromastes*, the corium is crossed by four longitudinal veins, not counting the analis, which borders the clavus anteriorly. By reference

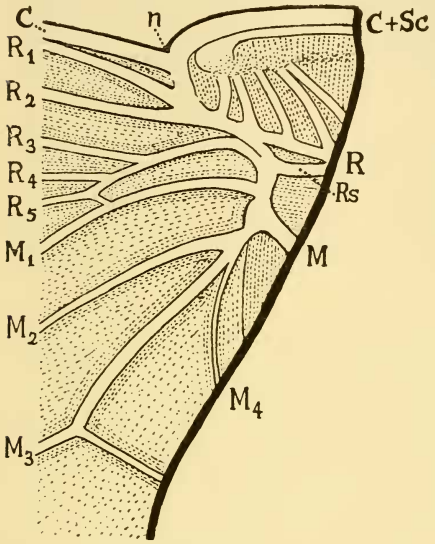
to the precedent tracheation, these veins are shown to be the subcosta, radius, media, and cubitus respectively. As in most Heteroptera, the subcostal trachea lies close up to the costal border; in the imago, the subcostal vein becomes more or less fused with this border. The radius and media are fused for some distance from their bases, and then diverge gradually at an acute angle. The cubitus is a separate vein, lying about halfway between the media and analis.

Having made the above comparison with *Syromastes*, it now becomes an easy task to name the radius, media, and cubitus in the corium of *Dunstaniopsis*. This is shown in Text-fig. 18. Owing, however, to the bad state of preservation, in this fossil, of the dividing line between corium and membrane, we cannot proceed to name the numerous veins in the latter area with any certainty. Here, however, we may fall back upon the type-specimen of *Dunstania*, in which there is just enough of the corium preserved to enable us to make the necessary connections.

In my original description of *Dunstania*, I paid little attention to this part of the wing, believing it to represent only a small flattened-out portion of the thorax of the insect. I now give, in Text-fig.19, a careful drawing of the region of the node and dividing line in this fossil. From the figure of *Dunstaniopsis*, it will be seen that R and M, after diverging from one another in the middle of the corium, again begin to converge, and are then unfortunately lost in a break in the rock-surface. In *Dunstania*, however, we are able to pick up these two veins as they approach the dividing line. R is seen to be just dividing into R_1 and Rs, while M converges towards the latter as a stout vein from below. Sc is fused with the costa, as in *Dunstaniopsis*. Between Sc and R there are a number of oblique ribs, half fused into the corium; these can also be seen in *Dunstaniopsis*, further basad along the same area.

Just before the level of the node, Rs turns upwards, and partially fuses with R_1. From the combined stem thus formed, three branches pass out into the membrane, viz., R_1, R_2, and R_{3+5}. Of these, R_1 is a short vein lying close alongside the costal margin, and supporting it from below; it ends up at about one-

third of the length of the membrane, upon the costal margin. The second branch, R_2, is a longer, gracefully curved vein, running below R_1 and parallel to the costal margin for most of its length, and finally curving up to meet the margin at about two-thirds of the length of the membrane. The last branch, R_{3-5}, gives off R_3, close to its base, and immediately after divides into R_4 and R_5. R_3 passes in a gentle curve beneath R_2, and ends up just above the apex of the wing. R_4 and R_5 meet again (in *Dunstania* only) beyond the middle of the membrane, and from there on continue straight to the termen as a single vein R_{4+5}. In *Dunstaniopsis*, R_{4+5} is a single unbroken vein from its origin to its termination.



Text-fig. 19.*

Returning to the corium of *Dunstania* (Text-fig. 19 and Plate lix., fig. 15), we can pick up M converging towards R as it approaches the membrane. On the dividing line, it is connected with R by a short, stout cross-vein, forming portion of the dividing line itself. From the swollen root of M upon the dividing line, two branches pass out into the membrane. Of these, the upper, M_1, arches gently upwards, so as to approach close to R_{3-5}, and is connected with R_5, just distad from its origin, by a short cross-vein. Thence onward, M_1 runs with a slight double-curving to the termen. The lower branch, M_{2+3}, almost

* Region of node and dividing line in hemelytron of *Dunstania pulchra* Till., showing the small anterior portion of the corium preserved in the fossil; (×7·5). Upper Triassic, Ipswich, Q.

immediately divides into two; of these, the upper, M_2, runs to the termen on a similar course to that of M_1, but well below it; while the lower branch, M_3, diverges from M_2 for some distance, until it gives off a backwardly descending vein, whose destination cannot be followed out in *Dunstania*; at this point, M_3 is bent at a very oblique angle, and passes on probably to near the tornus of the wing.

From the base of M_3, in *Dunstania*, a very weakly indicated vein, M_4, can be made out, passing downwards, about midway between M_3 and the dividing line; it can be seen to be converging towards the cross-vein mentioned in the preceding paragraph; but the fracture of the rock hides its further course from our view.

In order to follow out the further structure of the wing, posteriad to the region of M, we must now turn again to *Dunstaniopsis* (Text-fig.18), in which most of this part of the wing is fairly well preserved. In this genus, we can easily pick up the cubitus, running with a gentle curve upon the corium, well below M. In *Syromastes*, we see that M and Cu are connected by a short cross-vein, not far from the dividing line. In *Dunstaniopsis*, Cu gives off an oblique anterior branch, which approaches closely to two oblique posterior branches given off by M at about the same level; these two branches of M unite close to the dividing line, at a point where the branch from Cu lies very close below them. Here there is a break in the rock-surface; but we can pick up, on the other side of the break, a single weak vein curving into M_4. This is evidently the prolongation of the united branches from M and Cu.

Turning now to the main stem of Cu, we can follow it, in *Dunstaniopsis*, up to the dividing line between corium and membrane, where it gives off an oblique anterior branch, Cu_{1a}; this branch meets M_4, the weak vein already mentioned as descending from the base of M_3. At the angle formed by these two, which is almost a right angle in *Dunstaniopsis*, a third vein comes in from the membrane; following this distad, we see that it arises from M_3, which, in this genus, is a straight vein running to near the tornus of the wing.

We can now complete this part of the wing in *Dunstania*. The descending vein from M_3 must be the homologue of the corresponding vein in *Dunstaniopsis*; the only difference is in the angle of departure from M_3. On this difference, as well as upon its more numerous and slightly more divergent veins, we see at once that *Dunstania* had a broader and shorter membrane than *Dunstaniopsis*.

Following the main stem of Cu, which I call Cu_{1b}, across the dividing line in *Dunstaniopsis*, we see that it continues in a gentle curve, until it ends up on the dorsum of the wing, not far from the tornus. Below Cu_{1b}, another branch of Cu, Cu_2, arises on the dividing line, and passes into the membrane as a curved vein running to the dorsum below Cu_1.

The dividing line hereabouts is not well preserved, but its ending up on the dorsum can be just made out. The division between corium and membrane is clearly noticeable in the fossil on account of the difference between the colour of the rock and the fossil itself. The former is a dark grey; the latter a pale brown. The whole of the corium is coloured pale brown, and is flat and smooth. The membrane, on the other hand, is varicoloured, showing pale veins bordered by narrow bands of dark brown pigment, and, between these, areas of the darker rock-colour on those parts where no veins are present. Also, the membrane is lightly pitted all over, whereas the corium is quite smooth in this genus.

Sufficient will now have been said to make it abundantly clear that we have, in *Dunstania* and its allied genera, a primitive type of Heteropteron, of large size, and very probably of amphibiotic habits. From recent Heteroptera, such as the *Lygæidæ* and *Pyrrhocoridæ*, in which some of the venation is still preserved upon the corium, the *Dunstaniidæ* differ in the incompleteness and tortuosity of the dividing line between corium and membrane; and they show us how the anterior portion of this dividing line has been evolved, apparently in a most complicated manner, from a series of cross-veins and branches of main-veins linking up at different angles. The process by which the straight division between corium and membrane, found in most recent

Heteroptera, has been evolved from the stage seen in the *Dunstaniidæ*, is simply one of reduction and alignment of parts. When it is completed, as in recent *Pentatomidæ*, the clue to the venation of the membrane would be quite lost, were it not for the preservation of the tracheæ in the nymphal wing. I have not been able to find a single existing type of Heteropteron in which this venation is at all closely comparable with that of *Dunstania*. In the aquatic forms, especially, there does not seem to be any clue at all. Judging chiefly by the shape of the wing, and the condition of the venation of the corium, I am inclined to regard the *Coreidæ*, *Lygæidæ*, and *Pyrrhocoridæ* as the nearest relatives of the *Dunstaniidæ* at the present day. These three families, and no doubt also the *Pentatomidæ*, may well lie almost in a direct line of descent from the *Dunstaniidæ*. We should have to suppose, in restoring the latter, that the development of the scutellum had advanced very little beyond a normal size; and consequently, that the clavus, which, in the position of rest, borders the scutellum, was also very short. As no anal vein or clavus can be seen in the preserved portion of the hemelytron of *Dunstaniopsis*, this was almost certainly the case.

In Plate lix., fig.15, I offer a restoration of the complete hemelytron of *Dunstania pulchra* Till., based upon the preserved portions of the type and of *Dunstaniopsis triassica*. The poorly preserved *Paradunstania affinis* has not been brought into the discussion at all, and its only use in the restoration is to indicate the course of the wing-border below the tornus.

It now remains for me to revise my original definition of the family *Dunstaniidæ* in the light of our new knowledge, and to give definitions of the type-genus, and of the two new genera here proposed, and descriptions of the new species.

Order **HEMIPTERA.**

Suborder **Heteroptera.**

Family DUNSTANIIDÆ.

Large bugs, with hemelytra more than 30 mm. long. Hemelytron suboval, about half as wide as long, the corium either smooth or lightly pitted (hairy), the membrane pitted (hairy).

Veins present on the corium are R, M, and Cu; no clavus visible in the preserved portion, but the base of the wing is incomplete posteriorly in all known specimens. Sc fused with costal margin. Costa broken between corium and membrane by a strongly developed node. Dividing line between corium and membrane crosses the wing from node to antinode in a very irregular manner, being formed anteriorly by short cross-veins and portions of main veins, posteriorly by a sinuous line not made up of veins. On the membrane there are either eight or nine longitudinal veins, of which either three or four arise from R, three from M, and two from Cu; these veins runs distad in a slightly diverging manner, R_3 ending up at or near the apex, and Cu_1 at or near the tornus. From M_3 a downward and backwardly running branch passes to the dividing line, where it meets the intersection of M_4 and Cu_{1a}. Few cross-veins present on membrane. Veins of the membrane pale, generally bordered on either side by a band of dark brown pigment. A fairly broad border without pits, and probably coriaceous, runs completely round the membrane.

Horizon, Upper Trias of Ipswich, Queensland.

The genera comprised in this family are *Dunstania* Till., *Dunstaniopsis*, n.g., and *Paradunstania*, n.g.

Key to the known genera of *Dunstaniidæ*.

	M_1 connected with the lowest branch of R by a short cross-vein, not far distad from the dividing line	1.
	No cross-vein present at this level between M_1 and lowest branch of R	*Paradunstania*, n.g.
1.	Four branches of R crossing the membrane, viz., R_2 to R_5; R_4 and R_5 unite a little beyond half-way, forming a closed cell	*Dunstania* Till.
	Three branches of R crossing the membrane, viz, R_2, R_3, and R_{4+5}; the last a single straight vein connected with M_1 near its origin.....	*Dunstaniopsis*, n.g.

Genus DUNSTANIA Tillyard.

(Plate lix., fig.15, and Text-fig.19).

Membrane and a very small portion only of the corium preserved. Preserved portion of corium distinctly pitted all over. Membrane about as broad as long, the apex prominent but grace-

fully rounded. Node exceedingly prominent. R_1 a weak vein fused with costal margin from below node up to about one-third the length of the membrane. R_2 ending well before the apex, R_3 at the apex itself. Between R and M, at the base of the membrane, a closed cell is formed, bounded by the dividing line basally, by R_{3+5} anteriorly, by M_1 posteriorly, and by a short cross-vein connecting these two veins distally. Distally from this cell a second closed cell is formed between R_4 and R_5, these two veins at first diverging, and then converging to meet again at a point beyond the middle of the membrane. M_2 and M_3 united distally for a short distance upon the membrane. The backwardly projecting branch from M_3 comes off almost at right angles from the main stem. (Rest of hemelytron missing).

Genotype, *Dunstania pulchra* Till., (3, p.32, and Plate iii., fig.6).

Genus DUNSTANIOPSIS, n.g. (Text-fig.18).

Hemelytron completely preserved except for the extreme base of the corium (including the clavus, if present) and the apical portion of the membrane. A longer wing than that of *Dunstania*, and narrower in proportion. Differs from *Dunstania* as follows :—Corium smooth, membrane lightly pitted all over. Coriaceous border narrower and less defined; node somewhat less prominent. R_{4+5} a single straight vein, and hence no closed cell formed between R_4 and R_5. The basal cell completed by the presence of the short cross vein between M_1 and lowest branch of R is present, but is much shorter than in *Dunstania*. The backwardly projecting branch from M_3 to the junction of M_4 and Cu_{1a} comes off from the main stem at an angle of about 30°, and runs almost parallel to the posterior border below it. On the corium, M curves upward distally, converging towards R, and giving off posteriorly two branches which unite further distad and then meet an anterior branch given off from Cu; this latter vein divides at the dividing line into three branches, Cu_{1a}, Cu_{1b}, and Cu_2, of which the first runs to the intersection of M_4 and the backward branch from M_3. Cu_{1b} ends up at or near the tornus.

Genotype, *Dunstaniopsis triassica*, n.sp.

DUNSTANIOPSIS TRIASSICA, n.sp. (Text-fig. 18).

Greatest length of fragment, 31·5 mm.; breadth across the dividing line, 15·5 mm Estimated total length of hemelytron, 40 mm.

The specimen is only moderately preserved, and would appear to have been much torn distally before it became fossilised, since a part of a frond of *Thinnfeldia*, lying upon the same rock-surface, projects well into the gap where the missing distal portion ought to be, and is embraced on one side by the projecting torn costa, without appearing to overlie the wing in any way. Also the beautiful pattern of brown pigmentation bordering the veins of the membrane, though it can be seen to be present, is not by any means so well preserved as in *Dunstania*. The corium appears to have been hard, and is fairly well preserved; the veins lying upon it are not so distinct as those upon the membrane.

The venational characters being considered as of either family or generic importance, they will be found in full in the definitions given above.

Type, Specimen No. 107*a*, in the Queensland Geological Survey Collection.

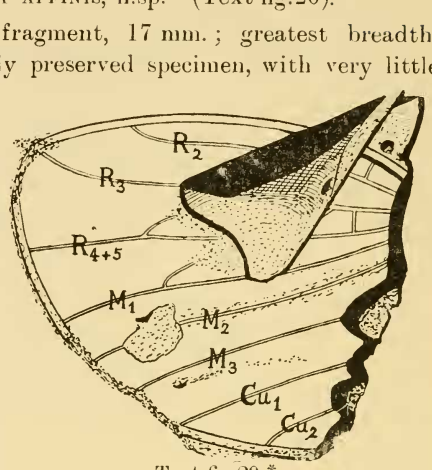
Genus PARADUNSTANIA, n.g. (Text-fig. 20).

Portion of membrane only preserved, and in very poor condition. Apparently a hemelytron of somewhat larger size than that of *Dunstania*. No cross-veins basally between M_1 and lowest branch of R. Cross-veins developed not far from dividing line between R_1 and R_2, and also between R_3 and R_{4+5}. This last vein receives a curved branch-vein from above, at about the same point as where, in *Dunstania*, R_4 and R_5 unite distally; but a break in the rock-surface prevents us from determining whether this branch is really R_4 or not. At about the same level, M_1 receives a curving branch from above; this branch appears to come from R_{4+5}, but its origin is not determinable with certainty. Rest of venation similar to that of *Dunstania*.

Genotype, *Paradunstania affinis*, n.sp.

PARADUNSTANIA AFFINIS, n.sp. (Text-fig.20).

Greatest length of fragment, 17 mm.; greatest breadth, 14·5 mm. A very poorly preserved specimen, with very little trace of the brown pigmentation bordering the veins. A large and deep triangular break has cut out a considerable portion of the courses of all the branches of R; the rest of the veins present can be traced out by the use of careful lighting.



Text-fig.20.*

This specimen appears to represent a hemelytron intermediate in size between that of *Dunstania pulchra* Till., and the much larger hemelytron of *Dunstaniopsis triassica*, n.g. et sp. In shape, also, it was probably intermediate between these two.

Type, Specimen No.147, in the Queensland Geological Survey Collection.

Note on the Origin of the Heteroptera.

In dealing with the phylogeny of the Order Hemiptera, Handlirsch(1, pp.1244-1249) rightly insists upon the clear-cut dichotomy between the two Suborders Heteroptera and Homoptera. Neither of these two Suborders can be derived from the other; for, on the one hand, the Homoptera have preserved the more primitive wing-form and venation, while, on the other, the Heteroptera have preserved the more archaic form of the head and antennæ. As the direct ancestors of both these recent Suborders, Handlirsch indicates some known Hemipterous fossils of the Upper Permian and Lias of the Northern Hemisphere, which he places in a distinct Order, Palæohemiptera, on the ground that it is not possible to demonstrate that they are definitely either Heteropterous or Homopterous. The Palæohemiptera he

* *Paradunstania affinis*, n.g. et sp.; (×2·8). Upper Triassic, Ipswich, Q.

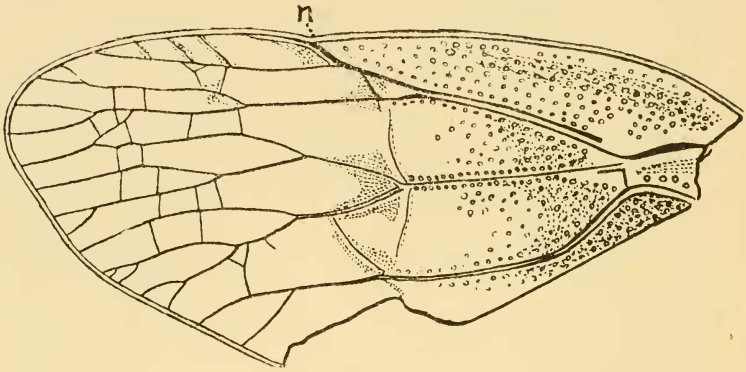
would, in turn, derive from the Lower Permian fossil genus *Eugereon*, which he places in a third Order, Protohemiptera.

Had it not been for the preservation of its mouth-parts, which form a primitive elongated sucking beak, *Eugereon* would never have been considered to have any relationship whatever with the Hemiptera. It was a huge insect, with primitive densely veined wings that were held out away from the body; the prothorax had lateral expansions suggestive of rudimentary wings, as in the case of some of the Carboniferous fossils. Apart from the dense venation, it is not possible to establish any close relationship between the venational plan of *Eugereon* and that of primitive Hemiptera; although it might be admitted that such a connection may possibly have actually taken place in the course of evolution, between *Eugereon* and the most densely veined types of *Fulgoridæ*, if the venation of the former had undergone a great deal of reduction and fusion of parts. That being so, it seems to me that the Protohemiptera are best regarded as a separate Order lying right off the main line of descent of the Hemiptera proper; the connection between the two being only establishable through a lost Carboniferous ancestor common to both.

The Palæohemiptera, on the other hand, are so obviously Hemiptera, that there seems to be no point at all in erecting a separate Order to contain them. Most of the Liassic fossils known are, in fact, definitely placed within the Homoptera by Handlirsch; and it is quite evident that they rightly belong there. Only the genus *Dysmorphoptila* Brodie, is retained within the Palæohemiptera; and, as this is probably a fragment, we may disregard it. Turning to the Permian fossils, we find two beautifully preserved wings, *Scytinoptera kokeni* Handl., and *Prosbole hirsuta* Koken, which are placed together in the Order Palæohemiptera. The former, I would regard definitely as an Homopteron; the latter most certainly combines the wing-characters of both Heteroptera and Homoptera, and could not well be placed in either Suborder without disregarding its evident affinity to the other. I propose, therefore, to sink Handlirsch's Order Palæohemiptera to the status of a Suborder within the

Order Hemiptera, this Suborder representing the original main stem of the Order, while the Heteroptera and Homoptera represent two distinct branches evolved from it.

Let us now compare *Prosbole* (Text-fig.21) with the restored wing of *Dunstania*, with a view to the establishment of a more complete phylogeny of the Heteroptera.



Text-fig.21.

Prosbole hirsuta Koken, hemelytron, after Handlirsch; (×2·1). Upper Permian, Kama River, Russia; *n*, node.

We notice, at once, that *Dunstania* is much more definitely Heteropterous, in that it shows the distinction between corium and membrane much more plainly than *Prosbole* does. Moreover, the corium of *Prosbole* is strongly pitted, while the membrane is smooth. In *Dunstania*, both are strongly pitted, while, in *Dunstaniopsis*, the corium is smooth and the membrane pitted. If, then, these genera had a common ancestor, it must have had a wing pitted all over, such as we find still preserved in many Homoptera. In most recent forms, the pits are swollen into tubercles, and no longer carry hairs; but there can be little doubt, from the nature of the pits in *Dunstania*, that, originally at any rate, they were the bases of insertion of macrotrichia. As we have already seen in the Protomecoptera, the macrotrichia were originally carried upon a dense meshwork of veinlets all over the wing. If, then, the wings of the Protohemiptera were also hairy, we are led to suggest that the true Hemiptera

diverged from them by a reduction of the original meshwork, in the course of which the pits, or bases of insertion for the macrotrichia, became seated upon the membrane of the wing; just as, in the Lepidoptera, the scales have appeared in a similar manner.

The original pitted wing of the true Hemiptera may be considered to have given origin directly to the various wing-types still extant amongst the older families of recent Homoptera: the main developments in this latter Suborder are not to be found in the wing at all, but in the specialisation of the head and antennæ, and in the development of the power of leaping. In this connection, we should bear in mind that a number of Homoptera, especially in the *Cicadidæ*, still show the dividing line between corium and membrane.

We have now to consider the origin of the Heteroptera. For this, we cannot take *Prosbole* itself as a starting point; but we must go back a little way beyond this type, and assume a closely similar ancestral form with a wing pitted all over. Keeping the *main scheme* of venation unaltered, we may now see the origin of the Heteroptera in a form in which the tendency of evolution in the basal half of the wing was towards *suppression* of the venation and hardening of the wing-membrane (with or without loss of the pits); while, in the distal half of the wing, the cross-veins of dense Fulgorid-like venation still preserved in *Prosbole* become obsolete, and the remaining venation becomes greatly altered, in correlation with the differentiation of the dividing line between corium and membrane.

I think that a very little consideration, aided by a comparison of the figures of *Prosbole* and *Dunstania* here given, must convince us that *Dunstania* represents a very typical immediate derivative from the hypothetical ancestor of *Prosbole*, from which we started in the preceding paragraph, along the lines there indicated as leading directly to the Heteropterous type. That is to say, *Dunstania*, though not directly derivable from *Prosbole*, is nevertheless closely related to it; but, while *Prosbole* itself cannot be accepted as having advanced along the line of the true Heteroptera, and must, therefore, be kept in a separate Suborder Palæohemiptera, *Dunstania*, on the other hand, has

advanced far enough to be considered a definite Heteropteron of a primitive type.

Let us now consider the very interesting question of the evolution of the dividing line between corium and membrane in the Suborder Heteroptera. *Dunstania* shows us this line in an exceedingly primitive condition. From it, we see that its anterior portion was originally composed of either branches of main veins, or cross-veins. But, as the main veins are all proceeding more or less distad, it is, therefore, inevitable that these various parts should meet at different angles, as we see so definitely shown in *Dunstania*.

The parts of the dividing line may be shown as follows, starting from the node or costal end (see Plate lix., fig.15, and Text-figs.18-19):—

A. Anterior Division, formed from cross-veins and branches of main veins:

1. The *node*, formed from the fused C and Sc.
2. Radial portion, formed from short parts of R_1 and R_2, partially fused together.
3. A short cross-vein connecting the radial portion with the median portion.
4. Median portion, consisting of a swollen root on M, from which the three branches of M are given off.

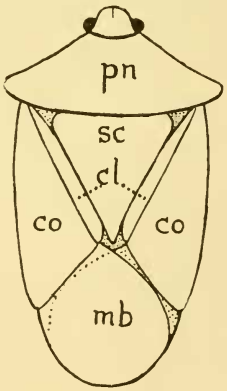
B. Posterior Division, consisting of a sinuous line crossing the wing more or less transversely, and not carrying either cross-veins or parts of main veins:

5. Medio-cubital portion, from the swollen root of M to Cu; the curvature of this part is concave to the corium.
6. Cubito-anal portion, from Cu to the antinode; the curvature of this part is slightly convex to the corium.

In the evolution of such a type as a recent Lygæid or Pentatomid Bug, all these diverse parts have to become aligned and fused into one harmonious whole. Probably a careful study of existing types amongst the Heteroptera would reveal many traces of the method by which this change has been brought about.

The other point of outstanding interest in the evolution of the Heteropterous hemelytron is the development of the clavus,

which is correlated with the growth of the scutellum. We are bound to assume that, in the original Hemiptera, the scutellum was of more normal size than it now is; and, consequently, the wings were not so completely folded over one another distally as they now are. In fact, we have to start from the normal type of scutellum and the roof-like position of holding the wings, still to be found in many Homoptera of the present day. From this, a gradual enlargement of the scutellum, together with a close folding-down of the wings upon one another, leads us to the condition found in recent Heteroptera. Here the dividing line marks the limit of the portions of the wing that are folded upon one another: while the anal area, or clavus, borders the two posterior sides of the large triangular scutellum. Thus we have to correlate the length of the clavus with the size of the scutellum, the tendency being towards enlargement as evolution progresses. Since, in *Dunstaniopsis*, there is no trace of a clavus in the preserved part of the wing, and the same is true of *Prosbole*, we have to conclude that both these forms had only a small or moderate-sized scutellum, bordered by a correspondingly short clavus, or even, perhaps, by scarcely any claval area at all.



Text-fig. 22.*

As soon as the overlapping of the two distal parts of the wing, or membranes, has been brought about, it will be clear that these two parts will in future act (while the insect is at rest) as one only; whereas the coria of the two wings remain separate. There will, therefore, be little tendency towards the thickening of the membrane at all, and the "heteroptery" might be expected to advance more quickly than ever. The line of evolution would then culminate in forms having a thick corium, from which all traces

* Diagram of a Shield-bug, family *Pentatomidæ*, to show the five parts of the shield, viz., 1, the pronotum, *pn*; 2, the scutellum, *sc*; 3 and 4, the right and left coria, *co*; and 5, the two completely overlapping membranes, *mb*. The clavus, *cl*, borders the scutellum on either side.

of venation had been eliminated, and a thin membrane, in which the veins were arranged more or less parallel to one another and to the wing-border. Probably the highest point reached by this line of evolution to-day is to be seen in the dominant family *Pentatomidæ*, in which the shield-shaped or "cut-into-five" appearance of the insect becomes perfected, and is often enhanced by bizarre sculpture and brilliant colouration. Text-fig. 22 shows the outline of such an insect, with the five separate areas of the shield-design named.

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EXPLANATION OF PLATE LIX.

Fig. 15.—Restoration of right hemelytron (forewing) of *Dunstania pulchra* Till., based upon the preserved portions of this fossil and of the allied *Dunstaniopsis triassica*, n.g. et sp.: (×5).

Lettering of Text-figures.

A, analis—C, costa—*c.b.*, coriaceous border—*cl*, clavus—*co*, corium—Cu, cubitus; Cu_{1a}, Cu_{1b}, Cu_2, its branches on the membrane—*m* or *mb*, membrane—M, media; M_1 to M_4, its branches on the membrane—*n*, node—*n'*, antinode—*pn*, pronotum—R, radius; R_1 to R_5, its branches on the membrane—Rs, radial sector—*sc*, scutellum—Sc, subcosta.